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PRESENT PROBLEMS IN PLANT ECOLOGY[1]

IV. Problems of Local Distribution in Arid Regions

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The physical conditions prevailing in arid regions are such as render it unsafe to admit without further investigation generalizations regarding their plant life which have been drawn from studies conducted elsewhere. This is sufficient justification of an attempt to analyze certain problems which confront the student of desert ecology in his efforts to apply knowledge or principles drawn from previous experience. These problems have the advantage of a certain clearness of definition, which corresponds in a way with the sharp features of the desert and its characteristic vegetation. Their solution may involve great difficulties, and some of them, with our present methods, may be incapable of solution, but they are, at all events, capable of clear statement.

In the attempt to present such a statement, which may or may not prove successful, I shall for the present limit the discussion to the desert country of the southwestern United States, for the sufficient reason that my own studies have been conducted in that region; and I shall omit all consideration of the higher elevations of the mountains, which, though in the desert, are not of it; so that whatever is said at this time will be understood to apply to the floor of the desert, that is the great plateaus and valleys which from Texas to California lie between the mountain peaks and ranges, together with the long slopes and low hills which border them on every hand and form the natural approach to the mountains.

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[1] A series of papers presented before the Botanical Society of America, at the Baltimore meeting, by invitation of the council.

Proceeding in a manner that will be indirectly a record of personal experience, one of the first questions presented to a student of desert botany is this: What are the conditions that determine the successful occupation of a desert habitat by certain plants, but prevent its occupation by others?

It will be necessary at the outset to understand what is meant by a desert habitat, since on this point the popular conception—and possibly that of some botanists—is not clear. There is as much difference between habitats in the desert as in any other region, possibly more, and their definiteness of location and relative sharpness of demarcation form one of the most striking and characteristic features of arid regions. The rivers of the valley trough, such as the Santa Cruz, the Gila and Salt Rivers in Arizona, though inconstant, are none the less the main drainage channels between the adjacent water sheds. Along their banks water-loving willows, cottonwoods and arrow-weed find a congenial home. The adjacent flood plain, with its water table within reach of their roots, is the natural habitat of the mesquite and some other semi-mesophytic species. Within its limits the areas known as salt spots are inhabited by various halophytes, especially by species of *Atriplex* and *Suaeda*. Just beyond the flood plain is the long slope, a most characteristic feature of desert topography, which rises slowly to the foot of the mountains, often miles away, its soil and drainage conditions presenting a sharp contrast to those of the flood plain, and its vegetation being correspondingly different. The low outlying hills, in their turn, present quite as marked peculiarities of soil, and furthermore introduce differences of aspect which are correlated with marked differences of vegetation. In short, the habitats of such a desert region as that of southern Arizona, as far as edaphic relations are concerned, present conditions which vary all the way from distinctly hydrophytic to extreme xerophytic, and all these may be in close proximity.

For all these habitats the fact is to be emphasized that the general climatic conditions are the same, and it is important to note that not a few of the plants which grow where a sufficient or even abundant water supply is assured are nevertheless marked, as a rule, as plants of an arid region by their coriaceous, hairy or otherwise xerophilous leaf structure. The point to be specially noted here is that while plants of the arid, or semi-arid southwest grow in a great variety of habitats, some of which are by no means dry, all are subject to the severe conditions of a desert climate, especially intense insolation, low percentage of atmospheric moisture, and drying winds. The problem, therefore, of the occupation of any one of these habitats is successfully met only by those plants that are already adapted, or are capable of individual adjustment to the dry air and hot sun in which they must live; all others inevitably fail.

This will be made clear by reference to the introduction, or attempted introduction, of various cultivated plants, a subject which presents a most instructive history. The yards of Arizona cities constitute an experiment station in which year by year, at private instead of public expense, the availability of one species after another for desert planting is being determined. From the great number of plants successfully cultivated there seems, at first sight, to be sufficient justification for the reiterated assertion that anything will grow here if you only give it water enough, but closer attention to the actual facts of the case makes it evident that this statement is true only in part, and that there are many plants that will grow only indifferently or not at all under the atmospheric conditions which prevail here, especially in the summer time. To give a few examples, geraniums, the universal easily raised plants of moister regions, are very uncertain, some varieties accommodating themselves fairly well to the desert air, while others fail altogether. Cannas and gladioli, which grow side by side in the east, part company here, the former making a good growth in

Arizona gardens, the latter failing altogether. Those who have handled roses for a period of years have learned what varieties may be expected to do well in the dry air of the desert, and what ones may be counted out, and so on through a long list of plants which, by knowledge gained in the costly school of experience, are coming to be depended on, or are being rejected one after another, as they are found to be unsuited to the environment into which they have been brought. Thus, in a purely empirical way, it has been found that many plants successfully cultivated in regions of greater atmospheric humidity make an entirely normal growth in the desert, if their roots are well supplied with water, but that others, however well cared for in this respect, either fail completely, or come short of making a healthy growth, and that this is especially true in the summer months when desert conditions are most pronounced.

With the accumulation of such facts the more evident does it become that a very complicated problem is here presented. Why is it that one plant, properly watered, does well in the desert, while another, though treated in the same way, makes a poor growth or fails altogether? At first thought it would seem as though there must be a difference in the capacity of the root systems of the two plants for absorption, and that this may be a sufficient explanation of their different behavior; but it is evident on consideration, that with precisely the same capacity for root absorption, a plant in which transpiration is successfully regulated may thrive in an atmosphere in which one subject to excessive transpiration will perish. The most elaborate experiments and the most exact determinations of rate of absorption—assuming that such determinations are possible—would be very likely to throw no light on the problem. Comparisons of the transpiration rate of the plants in question appear more promising, but the same difficulty arises in an attempt to pursue the investigation along this line, for there is no reason to suppose that two plants of widely different rates of transpiration can not successfully occupy the same habitat if their capacity for root absorption differs in the same ratio. But supposing that with infinite patience and with a reasonable approach to accuracy both sets of physiological data have been determined, we are still, quite possibly, entirely in the dark as to the real cause of the different behavior of the plants under investigation. It may be in their case that the whole matter of absorption, conduction, and transpiration is beside the mark, and that certain plants can not succeed in the desert because the intense insolation exerts directly a prejudicial influence to which they have not become inured. The intricate nature of the subject is apparent, and it is also evident that there is little encouragement for any one to take it up who has not had extended training and thorough equipment for physiological research. Yet with all its difficulties the problem is an attractive one, and the abundance of material to be had in any desert city, together with the great mass of data that has accumulated in the hands of horticulturists and at the experiment stations, offers the best of opportunities for extended and fruitful work.

If, as we have seen, the different deportment in the desert of plants growing, or having the opportunity to grow, side by side in well watered ground, is an exceedingly complicated matter, by how much are the difficulties increased when we pass from a habitat of uniform and highly favorable conditions, to the various and often extremely trying conditions which prevail in different neighboring habitats, such as the dry slopes underlaid by caliche, the salt spots and others. If the case of a plant growing in well watered soil may become desperate because of the scorching winds or the intense insolation to which its top is exposed, what hope is there for one that assays to grow where both dry air and dry soil present the supreme test of endurance? As a matter of fact only relatively few species meet the test successfully, yet there are some that do, and they present some of the most instructive data yet derived from the study of desert plants.

But little reflection is needed to arrive at the conclusion that the classical question regarding the relative importance of physical constitution and chemical composition of the substratum to plant growth—though like the poor it promises to be always with us—does not, and can not reach the heart of the problem. For every plant which successfully holds its place in a true desert habitat there is a delicate balancing of the regulation of transpiration, the power of absorption, the capacity of the conducting system, the presence or absence of storage tissues, and, we may well believe, the possession of protoplasmic properties which contribute to its powers of endurance. This being the case, it would seem that in future, investigations of the habitat relations, of desert species especially, must be directed mainly to the plant itself. The advantage of a thorough knowledge of soils is too obvious to call for comment, but it must be remembered that we are as yet only at the threshold of a greater and more promising work, namely, the investigation of the physiological requirements and capabilities of plants that can grow in a true desert habitat as compared with those that can not. In such comparative study lies, as it seems, the hope of real progress. It is impracticable for any investigator, at the present time, to mark out a straight path for others to pursue, and it would very properly be regarded as an impertinence were he to attempt this; yet there are certain obvious suggestions that may be offered.

In the first place, important results have already followed the simplest experiments and observations when these have been conducted with exactness and with a definite end in view. To refer to a specific case,—Professor Thornber, of the University of Arizona, undertook a few years ago to compare the habits of certain desert plants as regards germination. It was found that while the seeds of some species germinated at a given temperature, others could not be made to do so until they had been subjected to temperatures approaching the freezing point. These latter were seeds of winter annuals, and by this method a fundamental physiological difference between them and the summer annuals was established. Doubtless an indefinite amount of instructive and necessary work remains to be done in this direction, but the key to the situation was found in carrying out the simple experiments described. Again, partly as a relief from severer work, Dr. Cannon undertook, in the midst of his investigations at the Desert Laboratory, to map the distribution in the soil of the roots of some of the plants growing in the vicinity. Hardly was the work well in hand, and the root topography of less than half a dozen species mapped, when it was found that the clue to certain facts of distribution, blindly observed up to that time, had been discovered. I have spoken of this in more detail in another connection.

Obviously it is indispensable that determination of physiological data and of those belonging to the physical environment should proceed step by step together; and nowhere is this more strikingly true than in the investigation of soil relations. To refer to one more case of recent experience,—within the past year Dr. Livingston has determined the percentage of soil moisture present in soils obtained from each of the topographic areas of the Desert Laboratory domain and the adjacent flood plain of the Santa Cruz River. His studies were conducted independently, though naturally not in ignorance of ecological studies which were being carried out at the same time on the same ground. It now appears that a well-nigh perfect correspondence exists between the two sets of facts obtained by independent workers, so perfect, in truth, that a causal relation offers the only satisfactory explanation. The accumulation of physical data, however, has proceeded so far and so satisfactorily that the successful conduct of this line of investigation may be regarded as assured, but for the plant the relations are more complicated, and their investigation correspondingly more difficult. It seems likely that in the study of ecological relations from the side of the plant we shall employ more and more the methods and conceptions of physics and mathematics, but the fact is too patent to call for argument that neither now nor hereafter can these methods and conceptions be employed exclusively. In fact there has never been greater need than at the present time for exact observation coupled with correct judgment, and these can never be replaced or superseded so long as this department of botanical investigation continues to be cultivated. This will receive additional emphasis in the following division of the present paper.

The relations of desert plants to each other present a chapter, the importance of which has been unduly minimized until the general impression, even among botanists, seems to be that desert plants are to be studied only in relation to their physical environment; they are thought to grow so far apart, in ''open'' associations, that they are quite uninfluenced by each other's presence. Like other erroneous or incomplete conceptions, this may be true in part, especially where the most extreme desert conditions prevail, as for example in parts of the Colorado or Mojave Deserts, but in the great semiarid region of the southwest, taken as a whole, it is most misleading. The Desert Laboratory of the Carnegie Institution was located where it stands on account of the great natural advantages which the region and locality offer for the study of desert plants in place, yet I venture the assertion that over at least nine tenths of the area of the laboratory domain the establishment of a plant in the place which it occupies is conditioned quite as certainly by the influence of other plants as by that of the physical environment. It hardly needs more than simple observation to convince one that severe competition is the rule, though naturally its severity is heightened and the result hastened by the prevailing adverse physical conditions.

Beginning with some of the most obvious cases, the winter annuals of southern Arizona present an instance of as unmistakable competition of individuals with individuals and species with species as can be found in the eastern forest region of the United States. As the warmth of spring follows the winter rains the ground is thickly carpeted with *Amsinckia*, *Pectocarya*, *Bowlesia*, and various other herbaceous plants, which stand thick together and present to the eye the familiar crowding which is seen in a field of grain too thickly sown. Certain individuals dwindle and finally die, robbed of water, food and light by their stronger competitors. It might be interesting to repeat the experiment in the laboratory and to tabulate the results statistically, but it could hardly add to the conclusiveness of the demonstration. The same is true of the manifest competition of species with species, as seen for example in the occupation of relatively extended areas by some of the perennial grasses which, but for their presence, would certainly be covered, as the adjacent areas are, by a thick growth of other plants. Here the actual advance of the grasses from year to year may be observed, and such observations for the sake of more definite statement are now in progress on the Desert Laboratory domain. Convincing evidence of competition is thrust upon one's attention in passing from the desert to areas beyond its borders, and if the transition is abrupt, as for example on the western edge of the Salton Basin, where the desert abuts almost upon a mountain wall, the case is all the more striking. In this instance a straight course of less than five miles brings one from the actual desert, with its characteristic sparse growth of salt bushes, creosote bush, galleta grass, and the like, to the chaparral of the mountainside. Along the way the desert species fall out one by one, and are replaced by elements of the chaparral. As far as can be judged by their habits elsewhere and from their known range in altitude, there is absolutely no reason for this, except their inability to compete with plants of the chaparral, which, however incapable of normal development in the desert, hold their own ground, where the conditions are less strenuous, so tenaciously and completely that the desert species make no headway against them.

This, of course, is an interpretation merely, but with such an accumulation of evidence we are now in a position to proceed with the problem along definite lines with the expectation of definite results. Sowing together seeds of desert and other plants, the transference of individuals to denuded areas beyond their natural limits, and multiplied comparative observations of the deportment of different species on the ''edge of the desert'' are simple and obvious methods of procedure at the outset. Some of this work has already been done, enough to convince those engaged in it that in general the problem of the successful occupation of a desert habitat involves the recognition of actual competition on the part of its would-be occupants, a competition severe enough in some quarters to set up a barrier beyond which, in the midst of otherwise entirely favorable environmental conditions, they can not pass.

In their relations to each other, desert plants frequently exhibit not merely competition but accommodation. This has been clearly shown by recent studies of the root systems of certain cacti and other plants by Dr. W. A. Cannon. To take a striking example—superficial observation of the association of the sahuaro (*Cereus giganteus*) with one of the palo verdes (*Parkinsonia microphylla*) and some other shrubby perennials gives no satisfactory clue to the reason of this relation, and the common explanation that they are plants of similar biological requirements, and therefore grow together, is altogether inadequate and in part misleading. The careful study, however, that has been given to the root systems of these plants brings out the important fact that they grow close together by virtue of simple accommodation, which enables them to utilize to the utmost the scanty rainfall. The roots of the sahuaro are spread just beneath the surface of the ground, where they take up and promptly pass on to the storage cells of the trunk the water brought to them by every light rain. The roots of the palo verde, on the other hand, extend much more deeply into the ground, and are in a position to utilize the water which soaks down to lower levels after heavier rains. Thus the sahuaro profits by all rains, light and heavy alike, while its constant companion, the palo verde, is free from all competition on its part for the water which penetrates to lower levels. Much the same thing is seen on the flood plain of the Santa Cruz and other rivers, where the mesquite, with its deep roots reaching to the water table, is associated with *Bigelowia* and other plants, the roots of which extend to relatively shallow depths. In short, it appears that just as in a tropical forest the vegetation occupies successive "stories," so here the root systems of various plants habitually reach to different depths, and thus enable at least some species that would otherwise compete with each other to live in close and advantageous association.

From what has been said, it is evident that in the successful occupation of a desert habitat the mutual relations of the associated species play a highly important part. It is not quite easy at this stage of progress to point out the exact steps by which these complicated relations are to be determined and estimated; meantime the homely and effectual method of patiently gathering the data that are obtainable by careful observation is open, and as far as it has been pursued has yielded valuable results.

The broad general problem of the local distribution of desert plants is necessarily approached along the several lines that have been indicated. As we have seen, atmospheric conditions, whether of intense insolation or extreme dryness, that obtain in arid regions are limiting factors which many plants successfully meet, but to which many others succumb. There has been great need of more practical methods of determining and estimating the influence of atmospheric factors, and it is a matter of congratulation that the methods devised by one of the participants in this discussion, already widely in use in different parts of the United States, promise to meet this need to a degree that could not be hoped for at an earlier period. But it is never to be forgotten that under the same atmospheric conditions, and with equal chances in other respects, the deportment of two plants side by side, their capacity for adjustment let us say, is so different that the essential problem lies first of all in the physiological capabilities of the plant itself.

More strikingly true, if possible, is this seen to be the case when the relation of desert plants to the soil is considered. It is well that so much soil work has been done, that we have soil maps, that determinations of water capacity and other physical as well as chemical characteristics have been ascertained in so many habitats, and that we have a growing literature embodying observations of the relations of plants to underlying rocks, in short that the substratum has been the object of so long and so thorough study; there is no danger that we shall have too much of this, but there may be danger that we may sometimes forget to place the emphasis where it belongs, namely, on the fact that every species and every variety of plant is a law to itself in its relations to rock or soil. It is true enough that the different percentages of alkali salts at different distances from the center of a salt spot stand apparently in causal relation to the growth of different plants in corresponding concentric zones, but it is equally true that this zonal arrangement is also the visible expression of the capacity of these different plants to cope with the conditions there existing, and of this capacity, if it is to be expressed, as some day it must, in physical measurements, how inadequate is our knowledge. How greatly we need to really know the physiological constants, not of one but of many desert plants.

It is in the same line of thought, and with the same purpose, that I have referred to the inadequate conception according to which the relations of desert plants to each other have been so persistently overlooked or at least underestimated. It may now be set down as an established fact that over a large part of the arid or semi-arid territory of the southwest, competition on the one hand and accommodation on the other have much to do with the association of plant species and the density of the plant cover. Far more, it would seem, than has usually been thought, the character of various associations in this region is determined not simply by the physical but also by the living environment. More than ever too, it is plain that the path of progress lies in the direction of applying to the plant itself, in its natural surroundings, the experimental methods of the physical laboratory. Notable and fruitful beginnings have been made in this direction, but one who has attempted quantitative work with the sahuaro or ocotillo in the open need not be told that it involves difficulties not presented by seedlings of *Vicia faba* grown in pots, and that progress will necessarily be slow.

Thus far adjustment and adaptation have not directly entered into the discussion, although a moment's thought shows that all the paths along which we have come converge right here. If one variety of geranium flourishes in the desert air, while another by its side dwindles and dies, we can only say at present that the latter is not "adapted," or is apparently incapable of "adjustment" to the atmospheric conditions in which it has been placed. We find that plants growing in the wash near the Desert Laboratory do not, as a rule, succeed in gaining a foothold on the long slope leading to the hill near by; they are not adapted to the soil conditions there existing; but the creosote bush, which makes its home on these slopes, grows—thanks to its capacity of adjustment—even more luxuriantly in the wash than on its own domain. Similarly, certain plants of the salt spots grow better beyond than within their limits; they have become adapted to large percentages of alkali salts, but their capacity of adjustment is such that they grow just as well or better along an irrigating ditch carrying fresh water. Various other plants in the immediate neighborhood have not become adapted to the conditions prevailing in the salt spots, nor do they appear capable of adjustment to them, and accordingly are not found growing in such places.

We need not multiply citations of these familiar cases. Adaptation and adjustment have long been words to conjure with, out of the desert as well as in it, but we have made so little real scientific progress in the definition and determination of the things for which they stand, that some of our foremost students of ecology seem ready to abandon the effort, while others apologize when they use the terms, as if they were myths and had better be left alone. But nothing is gained, and much may be lost, by this method of procedure. We are face to face with a great body of phenomena of the most striking character, in connection with which these words are fittingly employed. We can not ignore the existence of the facts, and as scientific men we can not let them alone, while they insistently rise at every turn in our pathway and demand investigation. True it is that they bring in their train whatever is fundamental in biological inquiry —heredity, the direct influence of the environment, and differences in the properties of protoplasm in different plants. It is not customary, however, in laboratories worthy of the name, to shun investigations that approach to the deep mysteries of life. There is every reason why students of ecological problems should seek, not shun, this difficult but hopeful line of study. I say hopeful advisedly, for within the past three years there have come under my observation various definite cases of adjustment in plants, some of which have been accurately measured, correlated with external factors, and expressed by curves. Though essentially more difficult, there is no reason, as far as now appears, why the different degrees of adaptation of two species or varieties to a given external factor may not be similarly determined and graphically represented, as the expression of a definite difference of physiological activity, as shaped by heredity, in relation to that particular factor. Very little, as far as I am aware, has yet been accomplished in this direction, but it is a way that is wide open, and one that should attract those real investigators who, knowing difficulties, do not shrink from them.

We have considered in a way far from exhaustive some of the problems which specially interest the student of desert ecology, but which in their broader relations are not confined within geographical limits. In the efforts now being directed towards their solution the trend, as it appears to the writer, is not so much away from any previous form of thought or method as towards the wise and persistent use of every means that promises results. Progress is certainly being made in the direction of greater exactness; we are learning something of the possibilities of well-directed cooperation; and in these and other ways in which "science returns to the obvious"—to use the apt words of Francis Darwin—is an encouraging promise for the future.